

FOLIICOLOUS ASCOMYCETES 1: THE CAPNODIACEOUS GENUS SCORIAS REPRODUCTION¹

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ABSTRACT: *Scorias spongiosa* (Schw.) Fries development is analyzed by use of sequential collections from Georgia. The soma develops during the fall to winter season. The morphology of the anamorphic centrum remains unchanged as the soma matures. The teliomorphic centrum is dothideaceous; a sterile element in this centrum is interpreted as laterally positioned periphyses; the ascus is functionally bitunicate. A protocol to substantiate definite proof of reproductive state pleomorphism is discussed.

INTRODUCTION

Scorias Fries, a classic North American representative of sooty mold Ascomycete fungi, is known in the earliest American mycological literature. This capnodiaceous genus is based on an early known North American species, *S. spongiosa* (Schw.) Fries. This fungus occurs in a typical sooty mold plant-surface habitat in saprobic association with insect exudate. Although the distribution of the fungus is known to be along the U.S. east coast from northern Florida to Maine, *S. spongiosa* has received little attention since its initial impact on mycological literature of the 19th century.

The labyrinthic stroma formed by the dark mycelial growth, preceding pseudothecium formation, was first termed "sponge." Initially Schweinitz (1822) and later Fries (1829) in the type description of the genus, commented on the waxlike appearance of the mycelium and the change in the "sponge" matrix from brittle to soft upon absorption of moisture. The name *Scorias* was utilized by Fries to denote the stromatal resemblance to slag as the structure developed on leaves and branches of the American beech, *Fagus grandifolia* L. *S. spongiosa* was illustrated by Ellis and Everhart (1892) with a drawing showing ascocarps and pycnidia (as "spermogonia") originating from the same

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"fertile branch." They placed the monotypic genus in a taxon, the Perisporiaceae, defined with "ostiolum obscure or wanting . . . opening irregularly." Von Hoehnel (1910) described the hyphae as copious, partially slimy and fused together bundlelike. He characterized (1909) the pseudothecium centrum as cartilaginous-gelatinous due to the nature of the component sterile elements. Ascus dispersal was attributed to an apical swelling of the centrum. "Ein ausgesprochenes Ostiolum fehlt stets." Few other morphological insights can be gleaned from subsequent literature (i.e., Lloyd 1921; Batista & Ciferri 1963b).

This paper concerns the developmental morphology of *Scorias spongiosa*. A taxonomic monograph of the genus *Scorias* Fries is to appear later as an additional contribution from ongoing studies focusing on foliicolous fungi.

MATERIALS AND METHODS:

The sequential collections selected for detailed analysis represent periodic sampling from Athens, Georgia — i.e. LAM 200001 (25 X 1971), LAM 200004 (12 XI 1971), LAM 200006 (02 XII 1971), LAM 200007 (20 XII 1971). Collection LAM 200008 (21 I 1972) was utilized for illustration of mature material; information from collection LAM 200000 (18 VIII 1973) was incorporated for data on early development. Additional specimens examined from Georgia included LAM 200002 (02 II 1972), LAM 200004 (09 II 1972), LAM 200005 (20 II 1972), LAM 200009 (05 IV 1972), LAM 200010 (24 IV 1970), LAM 200011 (11 V 1972), LAM 200012 (11 V 1970) and LAM 200013 (10 V 1973). Other herbarium specimens examined included those from BPI (Brown VII 1932, Shear 4 X 1935, Shear 1 II 1903); CUP (Howard Cayuga Flora 48), FLAS (1862, 1863, 1864, 21183, 46426); ILL (Rogers 14-15 III 1958), Ellis, North American Flora (1363 a & b), Ravanel Fungi Americana (334 and 1877). Schweinitz collections from herbaria E, FH, K, PH and UPS were additional non-Georgian specimens examined.

Fresh material and 2% KOH revived dry material were cut on a Bailey freezing microtome and mounted in lactophenol or lactophenol-cotton blue; additional material was killed and fixed in FAA, paraffin embedded and the resulting sections stained with hematoxylin and methylene blue.

Camera lucida drawings were made by DRR; composite drawings from direct observation of sectioned material were done by F.E. Runyan.

RESULTS

THALLUS DEVELOPMENT

The general appearance of early thallus formation was as cream to buff colored tufts of mycelium on twigs and on some leaves of the American beech (LAM 200000). The fungus soma developed in accumulations of the exudate of the wooly aphid insect, which utilizes *F. grandifolia* as a host plant. Limited mycelial growth was seen on the ground at time of collection. The nonpig-

mented hyphae exhibited two distinct zones in the wall. In cross section of older hyphae (Fig. 1A), the outermost zone was widest, measuring an average 15μ . The outer boundary of the inner-wall zone was sharply delineated and measured approximately 1μ in diameter. The cell lumen containing the protoplast averaged 6μ in diameter. Cells were generally rectangular; size was variable (Fig. 1B). The outer-wall zone was present in the apical cell of presumed actively growing hyphae (Fig. 1C) and became wider in diameter than the inner-wall zone in cells progressively subtending the apical cell. The wall formed a constriction at sites corresponding to the location of septa traversing the cell lumen. In median cell focus, a centrally located gap could be detected in the isodiametric septa.

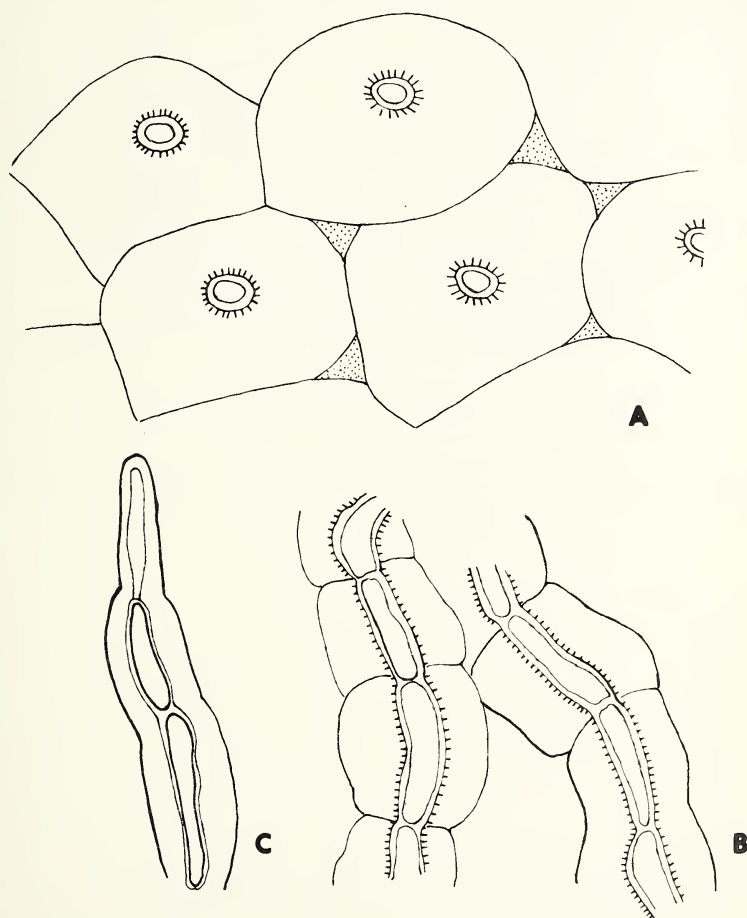


FIGURE 1. Hyphae. A. Cross section of hyphae, approx. 1300X; B. hyphae illustrating two wall zones, approx. 1000X; C. tip of young hypha, approx. 1000X.

Hyphal organization was effected largely by adherence of outer wall surfaces; reinforcement by cell fusions resulted in cytoplasmic continuity. Hyphae adhering together in small numbers for short distances, diverging individually or in small numbers and readhering with single or grouped hyphae, maintained a loose mycelial subiculum in localized areas on the supporting plant surface. The basic hyphal organization appeared as strands. Strand construction was similar throughout thallus development. The strand was usually rounded in a cross-section outline; the component hyphae were more or less parallel.

The somatic mycelium was well developed at a point in time represented by specimen LAM 200001. The hyphal wall construction was similar to that described in LAM 200000. The outer-wall zone measured 5-15 μ in diameter. An irregular verrucose deposition could be detected on hyphal surfaces in direct contact with other hyphal strands which were exposed to the atmosphere. The inner-wall zone measured approximately 1 μ in diameter. An interzonal area was identifiable which varied in width from almost nil to 1 μ ; it could be recognized by dark lines of varying length, oriented generally perpendicular to the axis of the hyphae, radiating from the outer surface of the inner-wall zone into the outer-wall zone. Pigmentation occurred first on exposed strand surfaces. The inner-wall zone of mature hyphal strands was initially achromatic and became darkened with a deposition of a pigment assumed to be melanin. The outer-wall zone was also initially achromatic and became darkened with a pigment similar to that of the inner zone, but of less intensity.

Mature stromata produced by the somatic mycelium of *S. spongiosa* had a definite internal structure (Figs. 2 & 3). Collection LAM 200013 is representative of mature stroma structure. It measured 11.6 cm in length and 5.5 cm at its highest point. Fig 2 is a diagrammatic representation of the stroma viewed lengthwise; Fig 3 represents a cross section at a level indicated by the arrow in Fig 2. The mycelial development radiated upward and outward from the supporting twig. The hyphae coalesced to form mycelial strands, which were

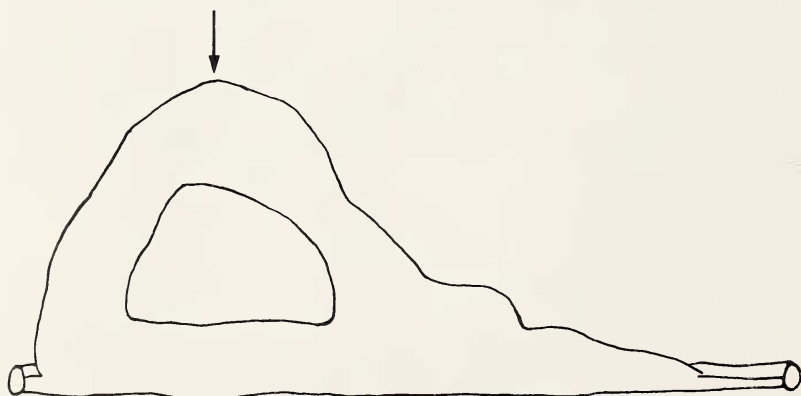


FIGURE 2. Diagrammatic representation of stroma lengthwise profile. Note enlargement of stroma in area represented by arrow in Figure 3.

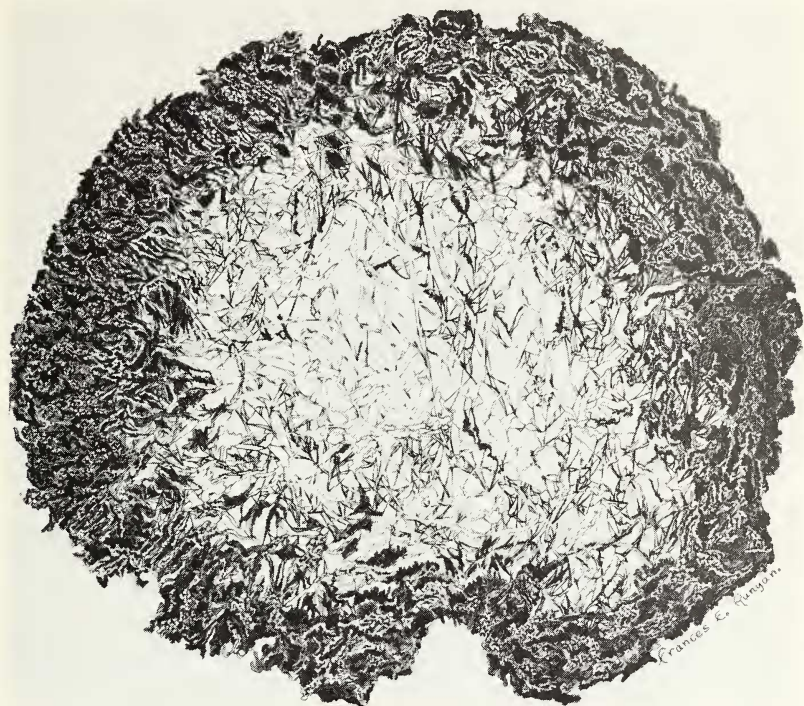


FIGURE 3. Cross-section view of mature stroma, approx. 3X. Supporting twig would be located at lower center portion.

largest in the lower center of the stroma. These central strands were formed in a lacunate region within the stroma which was also the highest portion (Arrow, Fig. 2; Fig. 3). Above the central labyrinth, the mycelial strands branched more frequently resulting in a compacted layer 1-2 cm deep, which formed the outermost region of the stroma. Reproductive structures ultimately developed on the exposed surface of the stroma. In the outermost compacted region of developing stroma, the hyphae comprising the outer layers of the component mycelial strands were fully pigmented; hyphal walls in the inner mycelial strand core were hyaline to yellowish. In mature stroma (Fig. 3) collected in late spring and bearing pseudothecia (LAM 200013), the strands in the outermost compacted portion were fully pigmented and most were surrounded by a nonpigmented layer representing the individual hyphae of new growth on the strand surface.

The dry stroma enlarged on contact with moisture. A rough estimation was made of structure modification upon wetting by calculating weight increase. Sections cut of collection LAM 200013 were weighed before and after wetting in a 10% formalin solution. An average 1.4% increase in weight was noted. Lack of appropriate material precluded confirmation of these data by use of additional stroma.

CONIDIOGENY

A phialidic anamorphic centrum was present at the tips of the mycelial strands in collections LAM 200000 and LAM 200014 on the cream to buff-colored tufts of mycelium (Fig. 4). Within the hyaline strand apex, the conidiogenous system was initiated by profuse transverse cell division in the centrally positioned parallel hyphae.

The short cells of the centrally located dividing hyphal strands were distinct from larger elongate cells of the hyphae in the outermost strand layers. Additional hyaline cells were produced from these short cells, which in turn branched toward the strand center. Sympodial branching was initiated from a site immediately below the apical septum and generally opposite a conidiogenous site (Fig. 8B). Limited apical expansion resulted in a branched system of phialogenic hyphae of one to several cells in length. Phialospores were produced from usually only one place on the conidiogenous cell near the uppermost septum, less frequently in the middle of the cell, or at the hyphal tip (Fig. 8A-E). No observations were made on initial spore development from living material. The first conidium was apparently formed as a small tubular protrusion which was blown out from the conidiogenous cell (Fig. 8A). Successive spores were produced through a collarette (Fig. 8D, E).

A dark brown pigment appeared in the inner-wall zone of the short-celled hyphae from which the conidiogenous centers were initiated, as well as in cells of adjacent strand hyphae with longer cells. The outermost nonpigmented hyphae of the strand apex was separated from the enlarged conidiogenous centers from this time on. Lateral expansion of the anamorphic centrum coincided with proliferation of conidiogenous hyphae and production of conidia; the conidia became compacted in the middle of the conidiogenous center, creating a locule. A necklike extension was developed beyond the sporogenous area by a convergence and elongation of a layer of dark strand hyphae surrounding a central cylinder of nonbranching sterile hyaline phialogenic hyphae. The outer darkly pigmented hyphal layer eventually ceased to grow; the hyaline inner layer of hyphae extended beyond the outer layer, became reflexed, resulting in what Batista and Ciferri (1963a) referred to as a fimbriated ostiole. Conidia appeared to be initially forced through a space between the hyphae of the hyaline core, thus creating a channel to the end of the neckline extension. These and subsequent conidia were exuded in a slimelike matrix which collected as a droplet at the apex of the neck.

The phialidic anamorphic centrum was present on the surface of the well-developed stroma; it was well represented in October collections as well as in collections from later in the year. Initiation of these conidium forming areas is identical to that described from collections LAM 200000 (Fig. 5); the resulting conidia were identical. However, the phialidic anamorphic centrum was formed in short mycelial strands of darkly pigmented hyphae which radiated from the stroma surface. The length of the subtending strand varied. None of these pycnidium-like structures was seen in this later stage to have an apical continuation of the outer mycelial strand hyphae into a necklike extension.



FIGURE 4. Asexual fruit body with phialidic anamorphic centrum, approx. 300X.

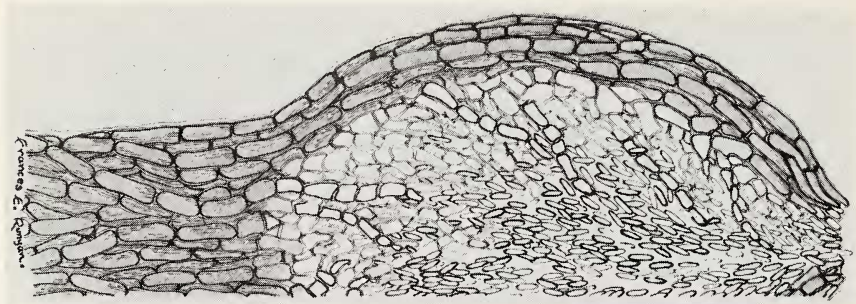


FIGURE 5. Asexual fruit body with phialidic anamorphic centrum, approx. 1000X.



FIGURE 6. Stroma surface detail illustrating ascocarps, approx. 30X.

ASCOGENY

Ascocarp formation was initiated by internal proliferation within a mycelial strand found on the stromatal surface (Fig. 6) and culminated in a prehymenial structure designated here the protopseudothecium. Eight or more individual hyphal strands from the surface network recoalesced in strand forma-

tion. Elongation of the strand appeared to be from the apical ends of the component hyphae. The mycelial strand organization was initially similar to that found in the central and compacted areas of the stroma, whereby parallel anastomosing hyphae formed into a rounded branch; the relative position of hyphae in the outer to central areas remained constant. All cells were found to be melanin-like pigmented. The onset of protopseudothecial differentiation was signaled by three areas of hyphal proliferation. A mycelial strand where a protopseudothecium was to be initiated was comprised of several hyphal zones; configuration patterns could be discerned in the outermost hyphal layers, in the middle hyphal layers and in the remaining innermost hyphae. The outermost layers did not depart from the basic parallel strand pattern (Fig. 7B). The hyphae in the middle layers began three-dimensional dichotomous and trichotomous branching. The cells were shorter but similar in cell shapes as compared to the outer most parallel hyphae (Fig. 7D). The hyphae in the innermost layers proliferated by formation of small isodiametric hyphae. These frequently branched, intermingled hyphae were generally oriented inwardly, perpendicular to the strand axis (Fig. 7E). All hyphae in the protopseudothecium had the basic 2-zone wall construction described earlier. Pigmentation developed in the outer layers containing the parallel, and the di- and trichotomously branched hyphae (Fig. 7B, C), but not in the isodiametric hyphae in the center of the protopseudothecial strand (Fig. 7D, E). Development of the outer layers of protopseudothecial strand kept pace with innermost core layer so that the pigment containing layers surrounded the inner core of hyaline isodiametric hyphae at all times. Proliferation of the latter and subsequent increase in width began in the lower portion of the protopseudothecium and became widest in the center of the ascocarp and terminated in an ostiole at the uppermost part.

Thus, the basic ascocarp subtended by a stalk (Fig. 7A) was formed before appearance of the ascogenous system. No further strand development appeared to occur after the inner core of hyaline hyphae was produced in the protopseudothecium. The portion of the protopseudothecial strand forming the ascocarp wall appeared plectenchyma-like in that the intertwined cells became affixed together, presumably by wall fusion. However, the centrally located nonpigmented hyphae retained their individual identity (Fig. 7E). In a longitudinal section of a protopseudothecium, the tissue might appear as pseudoparenchyma in both the wall and the central mycelial mass. This effect, as represented in the drawings such as those by Batista and Ciferri (1963b) for *S. spongiosa*, is due to the intermingled, highly-branched hyphae in the pigmented and nonpigmented layer in section showing the lumen of component cells from various angles separated by the wide walls.

The ascogenous system (Fig. 7F) appeared at the lower end of the pseudothecium. No ascogonium was detected; asci appeared to originate as croziers on proliferating ascogenous hyphae. Asci matured first in the center of the developing hymenium. The ascus wall was isodiametrically thickened only until the ascus mother cell elongated to full size. An ascus devoid of spores was cylindrical (Fig. 8F). The elongating ascus mother cells appeared to push up-

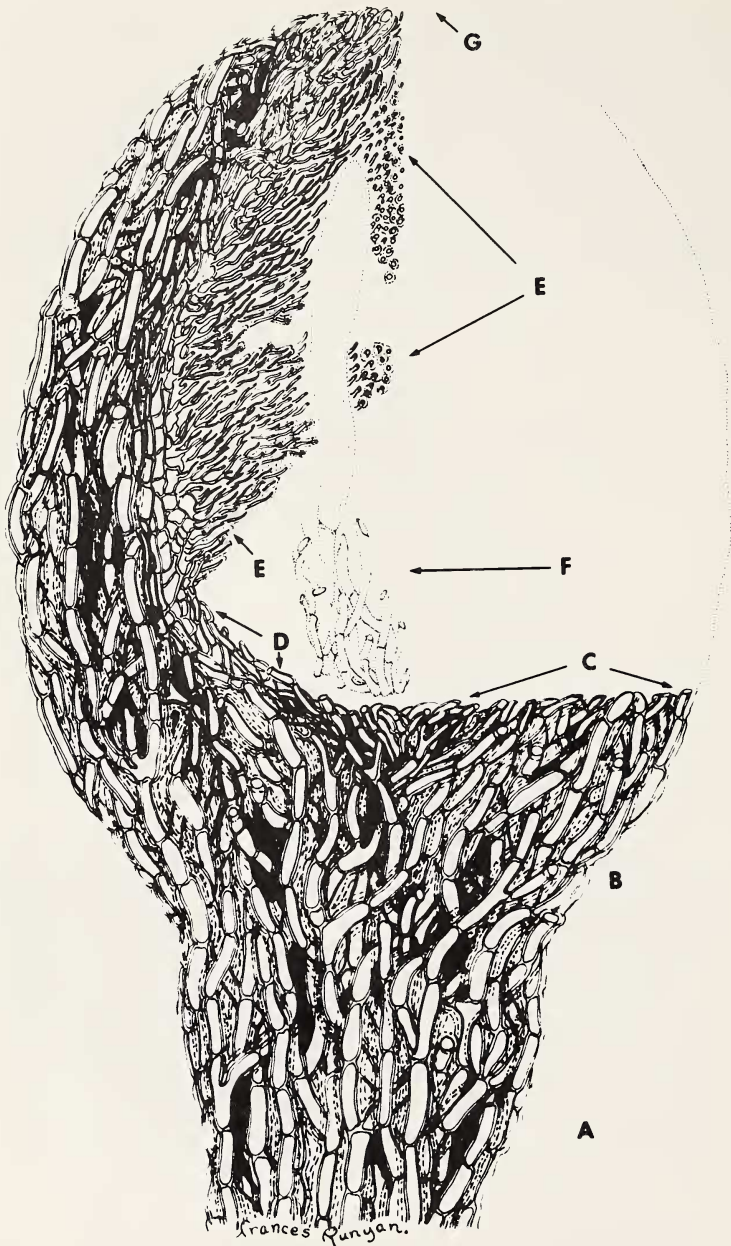


FIGURE 7. Ascocarp, approx. 1000X. A. mycelial strand subtending ascogenous center as stalk; B. base of ascocarp; C. dark tissue layer delimiting ascocarp; D. inner zone of hyaline hyphae; E. lateral periphyses lining locule; F. ascogenous hyphae bearing asci; G. ostiole.

ward among the nonpigmented hyphae occupying the center of the pseudothecium (Fig. 7). As the hymenium developed, the nonpigmented hyphae were displaced from the lower 75 percent of the original areas they occupied. The interface at the place of origin of nonpigmented hyphae with pigmented strand hyphae, effectively limited displacement. The resulting distortion created space within the pseudothecium (Fig. 7).

The shape of an ascus containing spores had been modified to obpyriform; the wall of such an ascus was thickened at the ascus apex with an evident *nasce apicale* (Reynolds 1971) and tapered in width toward the ascus base (Fig. 8G). Mature ascospores were hyaline and traversed by three septa. Discharged asci were found to have a discernible outer tunica surrounding a tubular inner tunica. Ascospores were frequently seen attached to the outer surfaces of ascocarps, some having germinated. No ascus was found to be discharged intact from the ascocarp as suggested by Ellis and Everhart (1892), although in some preparations, pressure applied to a coverslip would result in dislocation of individual asci and whole hymenia through the ostiole.

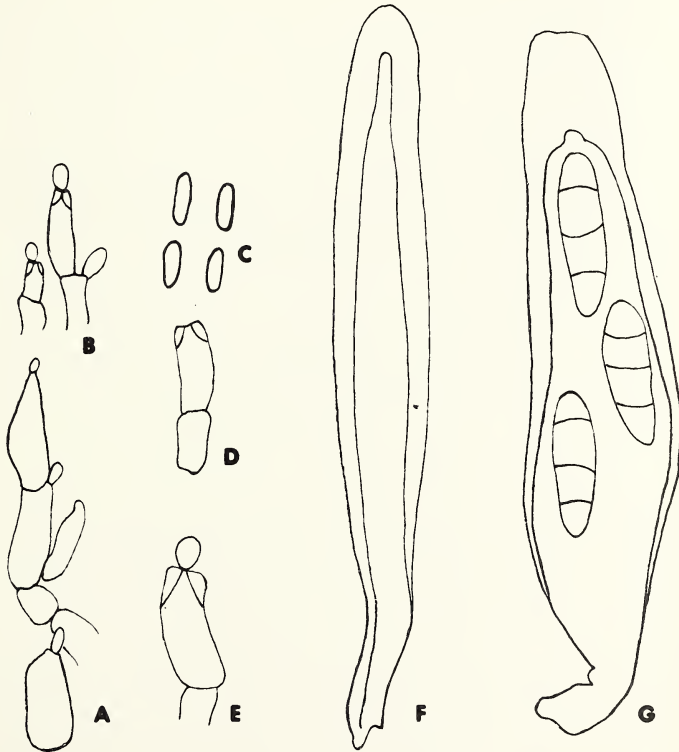


FIGURE 8. Phialides and asci, approx. 2000X. A, B. enterblastic monophialidic conidiophores bearing young conidia; D, E. phialides with collarettes; C. conidia; F. young ascus before ascosporeogenesis; G. mature spore-bearing ascus.

DISCUSSION

The terms teliomorphosis and anamorphosis have been introduced (Hennebert and Weresub 1977) in relation to a restatement of the International Code of Botanical Nomenclature, Article 59, "Names of fungi with a pleomorphic life cycle and of fossils assigned to form genera." These terms refer to basic reproductive modes of the holomorphic fungus and were defined as follows: teliomorphosis — "characterizing form that is involved in producing meiotic diaspores — in Ascomycetes, an ascocarp or its equivalent producing asci and ascospores. . . ."; anamorphosis — "The imperfect state . . . the asexual mitotic diaspore expression of a fungus . . ."

The term anamorphic centrum is utilized here as a Deuteromycete application of the Luttrellian Ascomycete centrum concept; this and other related terms are defined as follows: teliomorphic centrum = centrum sensu Luttrell (1951); anamorphic centrum = the reproductive or conidiogenous system component of an asexual fruit body; phialidic anamorphic centrum = an anamorphic centrum where the conidium is enteroblastically produced via a phialide.

The conidiogenous system described here consists of enteroblastic, basically monophialidic, conidiophores resembling that of two epimycotic Coelomycete genera. The illustrations by Seeler (1943) of *Eleuthoromycella mycophyla* von Hoehnel and especially *Eleutheromyces subulatus* (Fr.) Fuckel indicate strikingly similar acropleurogenous branched conidiophores. Both species are described as having wall tissue which is pseudoparenchymatous (textura angularia) rather than of parallel, somewhat gelatinized hyphae (textura oblita), as found in *S. spongiosa*. The pigmentation of *E. subulatus* is a nectriaceous burnt sienna, and that of *E. mycophyla* is carbonaceous. The walls of *S. spongiosa* pycnidia range from hyaline to melinoid.

Only one anamorphosis is associated with the life history of *S. spongiosa*. The term anamorphic centrum has been used to emphasize a continuity in terms of the conidiogenous system and the conidia produced in association with the stroma in all stages of development. Morphological forms of the asexual fruit body found here can be assigned to various pycnidial genera. Following Batista and Ciferri (1963a), these would be *Leptoxyphium* (globose, sessile, with no neck), *Podoxyphium* (globose stalked, with no neck) and *Microxyphium* (cylindrical, with a neck). Hughes (1976) speculatively refers to similar morphological forms as *Polychaeton* and *Conidiocarpus* (and perhaps *Scolecocyphium*). The position of the anamorphic centrum in the rapidly expanding and rounding mycelial strands (i.e., LAM 200000) would seemingly cause a cylindrical pycnidium-like structure. Continued growth of the surrounding hyphae would produce a "neck." This observation is made especially clear when conidiogenous systems are to be found centrally located in mycelial strands with the ostiole eliminated by the continued growth of the strand tip. The conidiogenous systems found in the more mature stroma develop at the ends of narrow hyphal strands. Unlike the pycnidia with a "neck," these strands extend from the surface of a stroma and terminate with the formation of the conidiogenous center.

Therefore, the generic concepts of these pycnidiaceous fungi as set forth in literature such as Batista and Ciferri (1963a) and Hughes (1976) are questionable; many of these appear to be based on growth cycle artifacts given undue taxonomic significance. Experimental data derived from pure culture work would go far in resolving the problem. Detailed observations on a chronologically obtained series of collections from a single natural locality, such as utilized in this study, may prove a valid alternative.

The teliomorphic type is modified dothideaceous. The ascus produced by *S. spongiosa* is functionally bitunicate; microscopic mounts reveal the nascent apical apparatus proposed by Chadeaud and explained by Reynolds (1971). The sterile elements peripherally produced from the wall, which hang into the locule, are not pseudoparaphyses sensu Wehmeyer. Therefore, in agreement with von Arx and Müller (1975), the concept of these structures as pleosporaceous (Corlett 1973), is rejected. These structures originate as outgrowths from the pseudoparenchymatous peripheral layer of the ascocarp locule and the ostiole. The term for these structures in an ostiole is periphyses. Because they are produced to a lower level in the ascocarp but are not attached in the hymenium as are paraphyses and additionally are not involved in centrum formation as are pseudoparaphyses, they are regarded as laterally positioned periphyses or periphysoids (Barr 1976). Samuels (1973) discussed centripetal paraphyses and apical paraphyses as found in unitunicate species.

In *Scorias*, as in other Ascomycetes, taxon definition is typed with the teliomorphosis. No Ascomycete species is known to produce more than one teliomorphosis sexual state, but many are known which produce one or more anamorphoses from the same mycelium or thallus. My attempts to work with *Scorias spongiosa* in artificial culture failed to yield the desired reproductive states. Instead, a hopefully acceptable compromise has been utilized involving sequentially collected herbarium specimens, which is similar to that utilized by Luttrell and Muthappa (1974). Holomorphic data was derived from collections taken periodically from a particular locality over a time span during which the fungus developed in nature. Additional and supportive information was derived from usual herbarium specimens available on loan from the institutions previously mentioned. Consequently, the author is reasonably convinced, in absence of definite proof sustained by data from artificial culture methods, that the stroma development is accurately presented for a localized strain of *S. spongiosa*, and that the reproductive states are likely to be those actually produced by the species, rather than being associated with the stroma of *S. spongiosa* by virtue of habitat preference of sooty mold fungi with similar morphological features.

Imperative in profiling the capnodiaceous whole-organism is an absolute certainty that the alternate reproductive states are biologically associated. Müller (1971), in a review of perfect-imperfect connections in Ascomycetes, pointed out that use of pure culture techniques has allowed definite proof of connections between the teliomorphosis and any anamorphoses produced by one organism. Biological connection of alternate states are definitely proved in

artificial cultivation, where this method is possible, by use of spore-to-spore cultivation, or by germination of one spore form to give rise to a mycelium in culture which produces an alternate state. Definite proof of biological connection is lacking, and only suspected, where demonstration of a single hyphal strand organically connecting several alternate states is found in randomly obtained herbarium specimens.

My concept of sooty mold fungi is derived from several thousand collections I have made in all of the neotropical countries and in some areas of the paleotropics, on the examination of all herbarium specimens I can locate which have been cited in the literature, and from attempts at experimental culture work with field-derived isolates. Consequently, I strongly advocate cognizance of the specialized microenvironment into which sooty mold fungi have adapted when systematic judgments are formulated as well as in the perception of pleomorphic or alternate reproductive state relationships. Therefore, especially in capnodiaceous fungi, systematic relationships should be determined from data derived from artificial culture of the species as well as from specimens collected in nature. Analytical analysis of the holomorphic sooty mold species demands a nonintuitive laboratory protocol in order that realistic taxonomic innovation can be made.

The intuitive "analytical analysis" of the interpretation of the sooty mold fungi was summarized by Hughes (1976). This viewpoint is in direct contrast to the rendering of systematic judgment which incorporates experimental data derived from a protocol utilizing pure culture techniques such as that demonstrated by Simmons (1969), or a chronologically obtained series of specimens from a single natural collection locality such as that utilized by Luttrell and Muthappa (1974). Hughes advocated *prima facie* establishment of alternate reproductive state association in the sooty mold colony as may be found in randomly collected herbarium collections. The *a priori* taxonomy proposed by Hughes (1976) contains the highly interesting, but biased, insight of a Fungi Imperfecti specialist. However, his philosophical commentary was unfortunately expressed in nomenclatorial jargon and, lacking experimental data, falls short of proper systematic documentation.

The annual growth and reproduction cycle detected in the sooty mold fungus *S. spongiosa* is regarded as indicative of efficient utilization of available microenvironmental resources under the influence of overall seasonal changes. This species and others in the family Capnodiaceae von Hoehnel exhibit morphological and life-history features, which would give advantages in coping with the stressful plant surface-atmosphere environment in which they exist. Thus, concepts of thallus and fruit body development should be justifiably influenced by habitat-related data. The sooty mold colony produced in nature by the capnodiaceous fungi should basically be regarded as an environmentally influenced association of species (Reynolds 1975; Reynolds and Pohl 1974). Any attempt at analytical analysis of the fungi in the plant surface microenvironment will have to be based on a convincing, nonintuitive demonstration of

biological relationships between teliomorphoses and anamorphoses of fungi which thrive in this habitat. Definite proof of these relationships is necessary because ultimately any patterns of reproductive state associations should be reflected in the taxonomy of these highly evolved Ascomycetes.

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